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Spatio-temporal variability in the cannibalistic behaviour of European hake *Merluccius merluccius*: the influence of recruit abundance and prey availability

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Cannibalistic behaviour of European hake *Merluccius merluccius* was studied through the analysis of 49 836 gut contents belonging to individuals from 6 to 82 cm in total length (L_T). Samples were collected every autumn between 1993 and 2009. The results showed that the consumption of conspecific individuals was consistent over space and time. The abundance, spatial distribution patterns and L_T structure of *M. merluccius* recruits were the main variables involved in *M. merluccius* cannibalism. A geographical pattern was found since increasing cannibalism was observed in areas of recruit aggregations. The L_T spectrum of recruits in autumn was also a key factor and dependent on the spawning period. When adults spawned from late spring to summer, an increasing cannibalism trend was found in autumn, due to the ideal size structure of the prey (*M. merluccius* recruits) for predators. Depth was also a significant variable, and a cannibal peak was detected at depths ranging between 50 and 200 m, coinciding with a spatial overlap of predator (pre-adults) and prey (recruits). The cannibalistic behaviour of *M. merluccius* began at *c.* 12 cm, although 75% were mid-sized individuals between 16 and 30 cm. Additionally, 90% of prey-hake were recruits <18·5 cm. Some biological and ecological aspects such as growth rate, spawning period, predation and competition interactions and the effect of some oceanographic events on *M. merluccius* cannibalism are also discussed.

Key words: density; feeding behaviour; recruitment; southern Bay of Biscay.

INTRODUCTION

Consumption of conspecific individuals in teleosts is a common and widespread phenomenon in marine and freshwater ecosystems. Research has shown that cannibalism in fishes may be a population survival mechanism when resources are scarce in the environment and that it may serve as a key recruitment control factor (Sale, 1982). In some cases, filial cannibalism has been related to an adaptive strategy in which parents consume some offspring to increase their future reproductive success (Klug, 2009). Cannibalism can also have an effect on fish population density and dynamics (Waldron, 1992; Persson *et al.*, 2000; Svenning & Borgstrom, 2005; Link *et al.*, 2012). The consumption of conspecifics has been connected to increased encounter rates between the prey and predator (Smith & Reay, 1991; Garrison & Link, 2000;

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Lappalainen *et al.*, 2006). For this encounter rate increase to occur (resulting in some degree of cannibalism), a geographical overlap of predator and prey is needed. Additionally, the degree of cannibalism may be affected by increasing densities of both predator and prey (Frankiewitz *et al.*, 1999).

The importance of European hake *Merluccius merluccius* (L. 1758) in food webs as a top predator has previously been established by many authors in different areas, and its feeding behaviour has been fully studied (Bozzano *et al.*, 1997; Velasco & Olaso, 1998; Cabral & Murta, 2002; Cartes *et al.*, 2004, 2009; Carpentieri *et al.*, 2005, 2008; Mahe *et al.*, 2007; Murua, 2010; Modica *et al.*, 2011). Although these studies addressed feeding strategies of *M. merluccius* in relation to seasonal, bathymetric and ontogenetic changes, other researchers have reported cannibalism to be a common and widespread feeding behaviour in *M. merluccius* and other hake species (Guichet, 1995; Bozzano *et al.*, 1997; Garrison & Link, 2000; Juanes, 2003; Mahe *et al.*, 2007; Link *et al.*, 2012). Cannibalism in *M. merluccius*, in the Bay of Biscay, appears to be influenced by the abundance of juveniles and by the overlap between distribution patterns of juveniles and adults (Velasco & Olaso, 1998; Mahe *et al.*, 2007), although factors controlling this event remain unclear.

Merluccius merluccius is one of the most important commercial fish species in the southern Bay of Biscay, especially in the Cantabrian Sea, where some nursery areas are located (Sánchez & Gil, 2000). The *M. merluccius* population in the study area has a protracted spawning season with peaks from January to March (Dominguez-Petit *et al.*, 2010). Egg production appears to be more influenced by environmental conditions and food availability than by energy body reserves, and it appears that reproduction in *M. merluccius* depends on energy consumed in the spawning period (Dominguez-Petit *et al*., 2010). Spawners usually concentrate on certain sites of the shelf break (Pérez & Pereiro, 1985; Sánchez, 1993; Murua, 2010). Eggs and larvae are mainly found in water temperatures between 10 and 12·5° C (Alvarez *et al.*, 2001, 2004; Ibaibarriaga *et al.*, 2007), and they retain a pelagic existence until they settle on the seabed after 50 days in the north-west Iberian region (Piñeiro *et al.*, 2008). The 0 year group are found in muddy bottoms, between depths of 70 and 200 m (Kacher & Amara, 2005), and are recruited into the population in autumn (F. J. Pereiro, F. Sánchez, F. & J. Fontenla, unpubl. data). *Merluccius merluccius* recruits are found aggregated in 20–35 km diameter patches along the Galician and Cantabrian Sea continental shelf (Sánchez & Gil, 2000). The patch sizes and their location over the continental shelf appear to be influenced by mesoscale anomalies that retain the larvae and juveniles.

Physical processes exert strong control over the distribution patterns of eggs and larvae of fish species (Koutsikopoulos & Le Cann, 1996; Sánchez & Gil, 2000; Alvarez *et al.*, 2001, 2004; Murua, 2010). The oceanography in the southern Bay of Biscay is highly influenced by both macroscale processes for seasonal time periods and mesoscale processes for the periods between seasons (Gil, 2008). Mesoscale structures could be very important in relation to biological processes, as they transport eggs and larvae, which in turn could be essential for the life cycle of some fish species. In addition, *M. merluccius* recruitment success has been associated with eddies in the Cantabrian continental shelf (Sánchez & Gil, 2000). The repeated presence of these eddies in the same areas is due to mesoscale oceanographic events and topographic factors, and these locations are where the main concentrations of *M. merluccius* recruits are found (Sánchez & Gil, 2000). This may be a consequence of larval aggregation within isolated mesoscale structures. Eggs and larvae must subsequently

be transported onshore (over the shelf) into the main nursery areas with favourable tidal, wind-induced and geostrophic current conditions. The oceanographic conditions that prevail during the early life stages are therefore of primary importance for the transport of eggs and larvae onto the shelf, to ensure survival and recruitment success.

The purposes of this study were to document trends in *M. merluccius* cannibalism observed in the last two decades and to investigate possible causes of changes observed. The main objectives were to establish the spatial and temporal relationships between *M. merluccius* recruit abundance and cannibalism and to identify the main environmental and biological variables that control the cannibalistic behaviour of *M. merluccius*. Some links between oceanographic conditions and the distribution of *M. merluccius* recruits and other prey are also discussed in relation to trophic interactions and variations in cannibalism. Knowledge of the mechanism underlying cannibalism is essential to obtain a better understanding of the dynamics in natural *M. merluccius* populations.

MATERIALS AND METHODS

FIELD SAMPLING

Bottom trawl surveys were conducted every autumn from 1993 to 2009 by the Instituto Español de Oceanografía (IEO) for demersal fishery assessment in the Cantabrian Sea (southern Bay of Biscay). These surveys followed a random stratified sampling scheme with three depth strata (70–120, 121–200 and 201–500 m) and five geographical areas (Miño-Finisterre, MF; Finisterre-Estaca, FE; Estaca-Peñas, EP; Peñas-Ajo, PA; Ajo-Bidasoa, AB) (Fig. 1). Some special hauls shallower than 70 m and deeper than 500 m were also conducted. The sampling unit consisted of 30 min tows during daytime at a speed of 5·6 km h^{-1} (3 knots). A BACA 44/60 bottom otter trawl (CARDOMAR S.L.; www.pesca2.com) with a mesh size of 10 mm in the codend, a width of 18·9 m and a height of 2·5 m was used. The bottom temperature and salinity

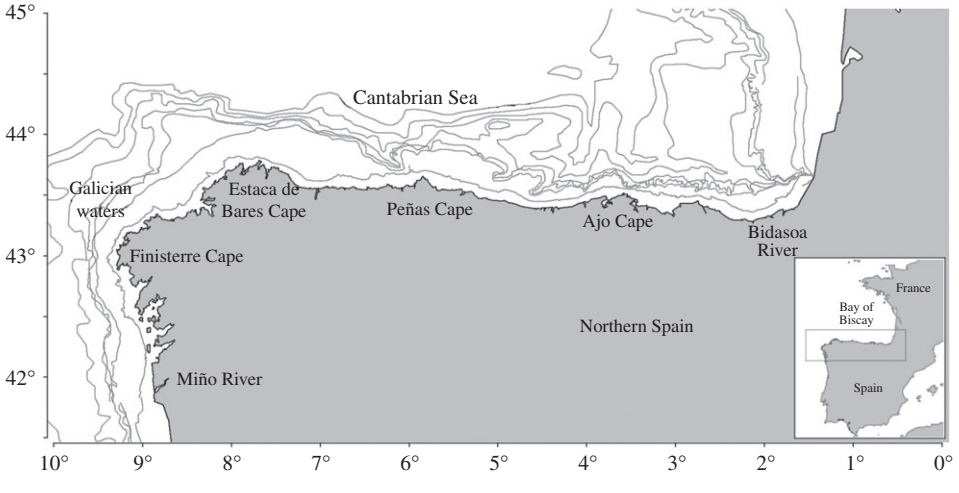

FIG. 1. Map of the study area showing main geographical features (rivers and capes) that represent the limits of the five geographical areas in the sampling design of demersal fishery assessment surveys. Bathymetric lines are also shown.

TABLE I. Summary of the total number of hauls conducted each year and the depth range from which *Merluccius merluccius* stomachs were analysed

	Number of hauls	Depth range (m)	L_T range (cm)	*N*	*n*	*%O*	*%N*	*%V*
1993	73	64–287	5–15	852	8	1·79	0·84	3·37
1994	95	59–461	6–14	2433	16	3·21	2·20	1·83
1995	92	44–575	8–11	2993	2	0·35	0·28	0·11
1996	94	44–571	8–17	2797	17	2·40	1·01	1·77
1997	95	53–560	5–21	3759	40	4·60	2·52	10·08
1998	93	50–580	12–19	3345	6	0·95	0·35	1·44
1999	98	45–668	14–14	2756	1	0·13	0·03	0·19
2000	88	50–566	11–15	2539	6	1·11	0·26	1·40
2001	84	47–579	11–27	2010	3	0·65	0·10	4·21
2002	87	47–601	6–14	1930	9	1·58	0·32	1·41
2003	90	42–562	8–14	2423	8	1·40	0·43	1·24
2004	95	47–680	8–25	3009	35	3·21	0·61	14·61
2005	101	50–598	5–17	3271	25	2·49	0·37	8·63
2006	101	54–609	8–18	3620	65	5·85	0·69	6·13
2007	103	49–696	4–20	3617	18	2·80	0·35	3·96
2008	116	45–608	5–24	4745	48	6·69	1·02	26·27
2009	108	44–613	7–17	3737	34	3·16	0·49	3·43
				49 863	341			

L_T, total length of prey; *N*, total number of *M. merluccius* analysed; *n*, total number of *M. merluccius* prey; *%O*, per cent occurrence of *M. merluccius* recruits in the total stomachs analysed; *%N*, proportion of *M. merluccius* cannibalism as a percentage in number; *%V*, proportion of *M. merluccius* cannibalism as a percentage in volume.

were also recorded at each haul position using a Seabird SBE-25 CTD (www.seabird.com; standard procedures were always around 5 m above the bottom every year).

STOMACH CONTENT ANALYSIS

During each haul, each of the *M. merluccius* specimens sampled was measured [total length (L_T) in cm] to clearly determine the mode of the population size. To analyse the stomach contents, 10 specimens were dissected per size range. Size ranges were based on the results of its feeding habits (Velasco, 2007), as follows: juveniles ($L_T < 9$ cm), pre-adults ($L_T = 10–35$ cm) and spawners ($L_T > 35$ cm).

For each specimen, the sex and stage of sexual maturity were also recorded. As part of the biological sampling, the gut contents were analysed onboard using a trophometer (Olaso, 1990) that consist of a set of graduated half-cylinders of different diameters for measuring the total volume of the stomach pellet. For regurgitated stomachs, the criteria described by Robb (1992) were followed, which included examining the state of the gall bladder. A full and intensely green-coloured gall bladder is indicative of an empty stomach, while an empty one denotes a full stomach where contents have been regurgitated. For each stomach, prey were separated and identified to the species level (whenever possible) and the percentage occupied by each prey in the total stomach content volume was measured. Prey were also measured when the digestion stage permitted it. Fresh prey or any items presumably consumed in the net were excluded from the analysis. A summary of the total number of hauls, depth range each year, size range sampled, total number of specimens dissected, total number of prey each year, the per cent occurrence of *M. merluccius* recruits (*%O*), percentage in number (*%N*) and percentage in volume (*%V*) is shown in Table I.

STATISTICAL ANALYSIS

The number of *M. merluccius* prey consumed per predator and year were followed to obtain a clear picture of the changes in *M. merluccius* recruits consumed during the study period (1993–2009). To analyse variations in cannibalism, two size ranges were established based on the size at which specimens are recruited to the bottom: $L_T < 20$ cm and $L_T \geq 20$ cm. To analyse direct relationships between recruit abundance in the surveys and in the stomachs, a Pearson correlation was calculated.

To analyse the spatial overlap of predator and prey, the accumulated frequency of occurrence of *M. merluccius* predator ($L_T \geq 20$ cm) and *M. merluccius* prey ($L_T < 20$ cm) was analysed along the study area (between 10 and 1° W). The frequency of occurrence of its main prey, blue-whiting *Micromesistius poutassou* (Risso 1827), is also shown.

Some biological and environmental variables were selected so that their global influence on *M. merluccius* cannibalism could be analysed. To identify the number of main explanatory variables involved in cannibalism, a generalized linear model (GLM) was constructed. The abiotic and biotic variables involved in the initial model included the following: year, nursery area, depth, bottom temperature, number of other prey in the gut contents [*e.g. M. poutassou*, anchovy *Engraulis encrasicolus* (L. 1758), horse-mackerel *Trachurus trachurus* (L. 1758) and crustaceans], presence of *M. merluccius* prey in the haul, total abundance and size range of main prey in the haul.

Four nursery areas were defined as a function of recruit density, corroborating the results obtained by Sánchez & Gil (2000). This factor has been treated as presence of cannibalism inside–outside each area.

Given the distribution of the response variable, a GLM with a Poisson distribution was proposed. For this distribution of residuals, the most suitable link function is the log function (McCullagh & Nelder, 1989).To determine the variables included in the final model, the level of significance of each variable and the improvement in the proportion of explained variability (Chambers & Hastie, 1993) were calculated using a stepwise procedure. To obtain the level of significance, the χ^2 of each variable was calculated, and those with P-values > 0·05 were rejected. The proportion of the variability explained by the final model was obtained using the quotient of the variation in the prediction and the true results as a proportion of the total variation. All analyses were performed with the software R for mathematical and statistical computing R 3.1.1 (R Core Team; www.r-project.org).

RESULTS

SPATIAL AND TEMPORAL VARIATIONS OF *M. MERLUCCIUS* CANNIBALISM

In this study, cannibalism in *M. merluccius* accounted for 5·2%*V*, 0·9%*N* and 0·7%*O* of the global diet. High interannual variability in cannibalism was found (Table I), with the highest %*V* values in 2008 (21·3), 2004 (15·1) and 1997 (10·1). The depth distribution of *M. merluccius* in the study area (Fig. 2) showed that the population inhabited the entire survey depth range. No distinct depth patterns between small and large *M. merluccius* were observed, although most of the specimens >40 cm appeared below 350 m depth.

The spatial distribution patterns of *M. merluccius* cannibalism appeared to be concentrated in certain areas (Fig. 3). Cannibalism mainly occurred between 70 and 200 m depth and inside and around the four nursery areas (Coruña, Ribadeo, Peñas and Guetaria) already described by Sánchez & Gil (2000). *Merluccius merluccius* distribution varied longitudinally in the Cantabrian Sea with four relative maxima at *c.* 8·5, 7·0, 5·5 and 2·3° W (Fig. 4), coinciding spatially with concentrations of *M. merluccius* recruits

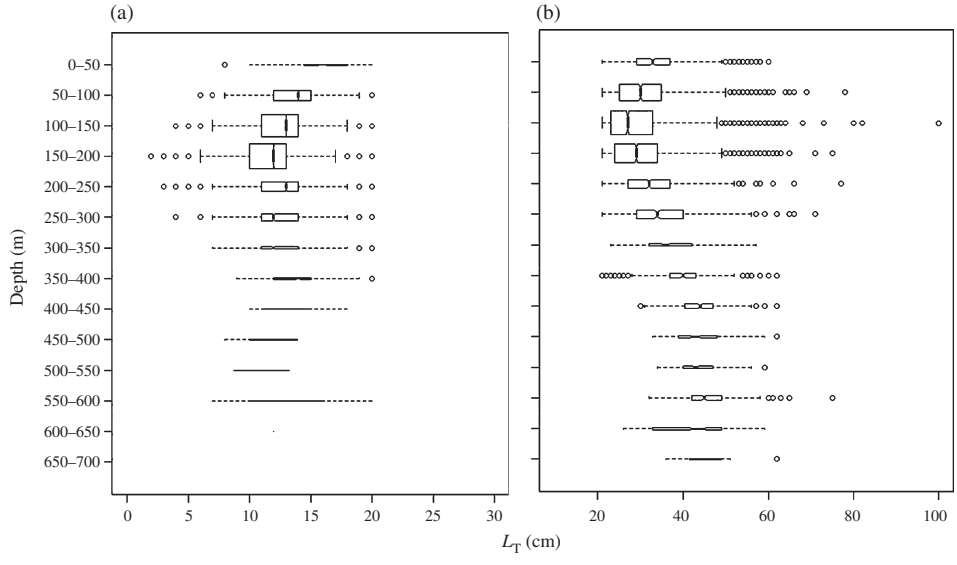

FIG. 2. Total length (L_T) distribution by depth of *Merluccius merluccius* recruits (a) $L_T < 20$ cm and (b) $L_T \geq 20$ cm. The smallest observation (minimum), lower quartile, median, upper quartile, largest observation (maximum) and outliers are indicated. The width of each box is directly proportional to the abundance.

and, interestingly, with their consumption by *M. merluccius* predators. A wider distribution across the whole study area, however, was found in *M. poutassou*, both in the surveys and in their consumption.

The temporal evolution of the *M. merluccius* recruitment index (specimens < 20 cm) showed great fluctuations among years (Fig. 5), with peaks in 1997, 2005 and 2009.

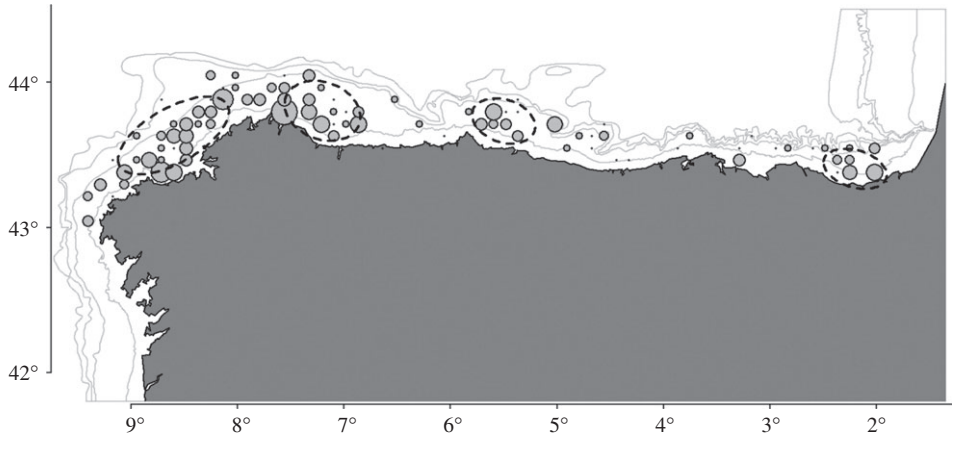

FIG. 3. Spatial distribution patterns of *Merluccius merluccius* cannibalism (1993–2009). Size of circles is proportional to the number of *M. merluccius* total length <20 cm found in the stomachs in each haul (the position of the hauls is the same every year). Nursery areas (_ _ _) found by Sánchez and Gil (2000) are also shown.

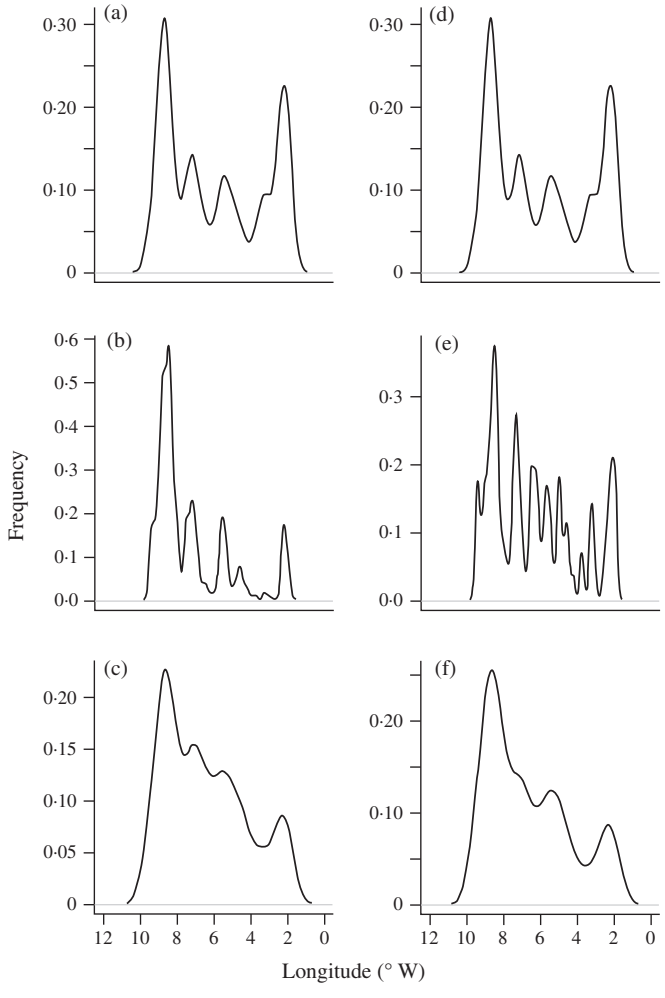

FIG. 4. Spatial distribution patterns in terms of frequency of occurrence of (a, d) *Merluccius merluccius* predators (total length, $L_T \geq 20$ cm), (b) *M. merluccius* recruits ($L_T < 20$ cm) in the surveys, (c) *M. merluccius* recruits ($L_T < 20$ cm) in the stomachs, (e) *Micromesistius poutassou* ($L_T < 20$ cm) in the surveys and (f) *M. poutassou* ($L_T < 20$ cm) in the stomachs. Data are integrated over the 17 years of study on the Cantabrian Sea continental shelf (between 10 and 1° W).

A significant correlation between recruitment and cannibalism was found ($r^2 = 0{\cdot}65$, $P < 0{\cdot}001$) for the time series from 1993 to 2005. When the relationship was studied for the entire period, however, no significant correlation was found, due to the anomalies of the last 4 years. Two peaks in *M. merluccius* cannibalism were observed in 2006 and 2008, even though both years had low recruitment.

When comparing consumption of conspecifics and consumption of its main prey (*M. poutassou*), it appeared that years of high consumption of *M. poutassou* displayed low consumption of *M. merluccius* recruits and *vice versa* (Fig. 6). No significant correlation, however, was detected ($r^2 = 0{\cdot}06$, $P > 0{\cdot}05$) suggesting that factors other than *M. poutassou* consumption might be controlling cannibalism.

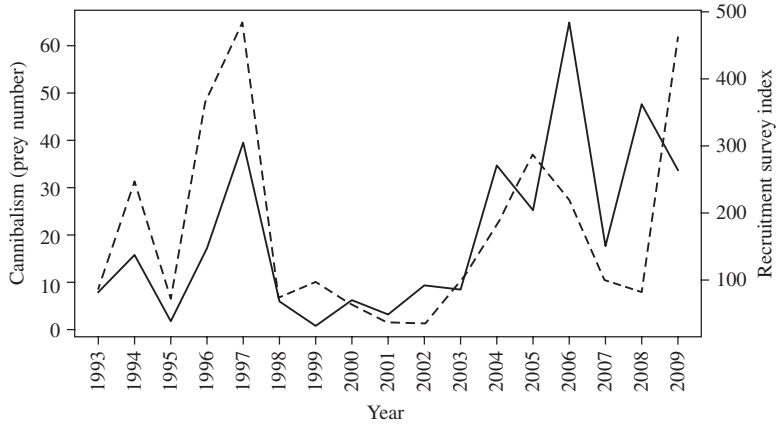

FIG. 5. *Merluccius merluccius* recruitment survey index (– – –) and *M. merluccius* cannibalism (——) between 1993 and 2009. Cannibalism is shown as the total number of *M. merluccius* prey. The recruitment survey index was calculated as the stratified biomass of *M. merluccius* recruits, total length, L_T, <20 cm (kg haul^{-1}) standardized to depth strata.

PREDATOR AND PREY LENGTH RELATIONSHIPS

The predator L_T and prey L_T relationship was examined using a linear regression model (Fig. 7). There was a significant and positive correlation ($r^2 = 0{\cdot}749$, $P < 001$) between predator (mainly *M. merluccius* pre-adults) and prey (*M. merluccius* recruits). Although *M. merluccius* began to feed on recruits very early (at *c.* 12 cm), 75% of the predators were specimens between 16 and 30 cm. Additionally, 90% of prey *M. merluccius* were recruits <18·5 cm, and 75% of prey *M. merluccius* were recruits between 9 and 15 cm.

The L_T distribution of *M. merluccius* recruits observed in the surveys, although with a slight difference, was significantly higher than that observed in the stomachs, with

FIG. 6. The consumption of *Micromesistius poutassou* total length, L_T, <20 cm (– – –) by *Merluccius merluccius* and *M. merluccius* cannibalism $L_T < 20$ cm (——) between 1993 and 2009. Total number of prey found (*M. poutassou* and *M. merluccius*) in the stomachs each year is shown.

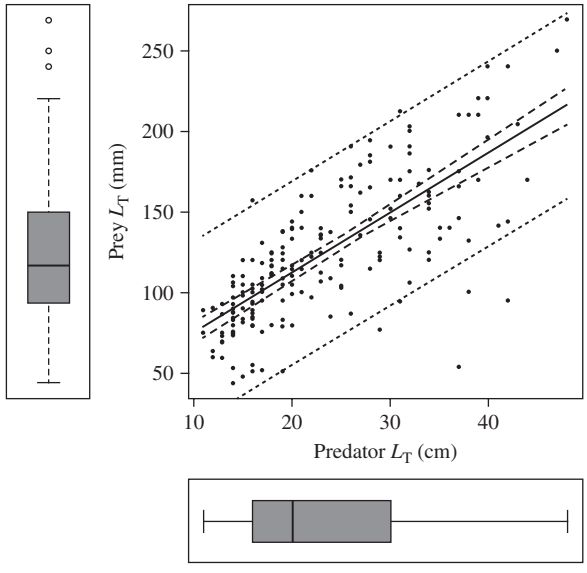

FIG. 7. Relationship between *Merluccius merluccius* predator total length (L_T) and *M. merluccius* prey L_T. The 95% C.I. (– – –) and the 95% prediction interval, PI (.....) and box plots of the L_T of predator and prey are shown. The curve was fitted by: $y = 3{\cdot}70x + 38{\cdot}27$; $r_2 = 0{\cdot}75$, $P < 0{\cdot}01$.

median values of 12 and 11 cm, respectively (Fig. 8). When observing trends in the size distribution along the whole historical series, some fluctuations arise (Fig. 9). More variability in size distribution of recruits in the stomachs was found. Except for the years 1998, 1999, 2000 and 2008, however, the preference over smaller individuals appeared to be consistent over time.

FACTORS CONTROLLING SPATIO-TEMPORAL PATTERNS OF *M. MERLUCCIUS* CANNIBALISM

The final formula of the GLM was: cannibalism = year + nursery area + depth + abundance of *M. merluccius* $L_T < 20$ cm, family = Poisson (link = log). The analysis of variance (ANOVA) for the final model is shown in Table II. The final model explains 25·30% of the total variation. Nursery area was the main factor involved in cannibalism intensity and explained the highest amount of the variability. This factor was created as a function of recruit density (presence of cannibalism inside–outside each area), suggesting the relevance of aggregations of *M. merluccius* recruits on cannibalism. Other significant variables involved in the model were depth and abundance of specimens with $L_T < 20$ cm.

DISCUSSION

In the study area, *M. merluccius* occupies an important role as a top predator in the trophodynamics of the fish community. The spatial and temporal variability in the *M. merluccius* diet reflects changes in prey availability and therefore an opportunistic

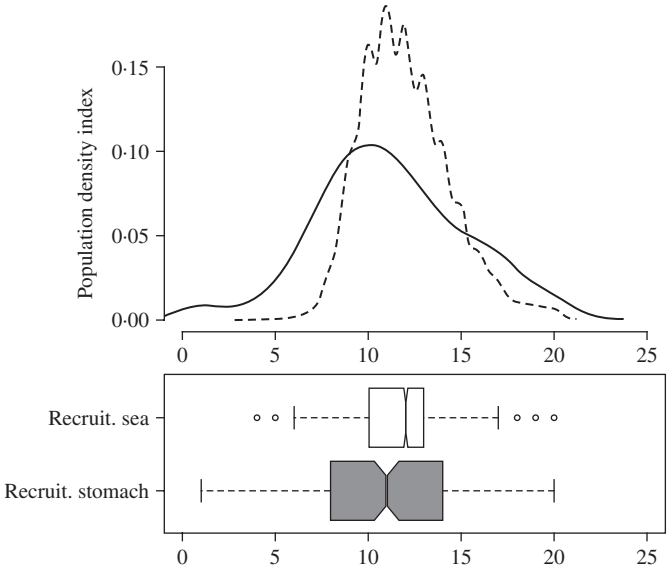

FIG. 8. Overall total length (L_T) distribution of *Merluccius merluccius* recruits ($L_T < 20$ cm) at sea (- - -) and *M. merluccius* recruits ($L_T < 20$ cm) found in the stomachs (——). Data were collected from trawl surveys between 1993 and 2009. Box plots of the size structure of *M. merluccius* recruits $L_T < 20$ cm are also shown.

feeding scenario (Waldron, 1992; Garrison & Link, 2000). The cannibalistic behaviour of *M. merluccius* is not an exception to this pattern, and the degree of cannibalism in this species appears to be strongly related with the availability of recruits and alternate prey. Although the present work has been focused only on one specific period of the year, it should be noted that the period of sampling (autumn) coincides with

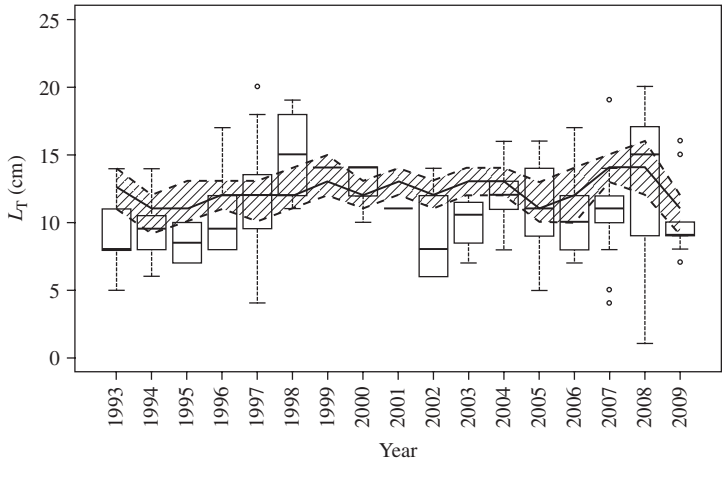

FIG. 9. Total length (L_T) distribution of *Merluccius merluccius* recruits ($L_T < 20$ cm) in the stomachs (box plots) between 1993 and 2009. ——, the median; □boxes, the interquartile range (IQR). Outliers (○) are also shown. ▨, the size distribution of *M. merluccius* recruits at sea, showing the median and the IQR.

TABLE II. Analysis of variance (ANOVA) results of the generalized linear model of *Merluccius merluccius* cannibalism by number. Deviance explained: 25·30%. Only significant variables are shown

	d.f.	Deviance	Residual d.f.	Deviance of residuals	$P(>\chi^2)$
Null			1576	1457·6554	
Year	16	233·257239	1560	1224·3981	$P<0·001$
Nursery area	4	146·899315	1556	1077·4988	$P<0·001$
Depth	1	30·848467	1555	1046·6503	$P<0·001$
Merluccius merluccius abundance < 20	1	30·202794	1554	1016·4475	$P<0·001$

recruitment period of *M. merluccius* in the study area, and therefore the maximum estimation of cannibalism is expected.

Merluccius merluccius cannibalism in the southern Bay of Biscay was consistent over time, with maximum values of 21%*V*. In the Celtic Sea, Mahe *et al.* (2007) found that *M. merluccius* cannibalism constituted 19·2% mass (%*W*) and 10·53%*O*, while Cartes *et al.* (2009) found higher levels of cannibalism (40%*W*) in the western Mediterranean Sea. Furthermore, Roel & Macpherson (1988) detected up to 100%*O* of the diet in some specific regions (and in a particular season) off the Namibian coast.

Fluctuations in *M. merluccius* cannibalism can be related to (1) variations in spatial overlap between predator (medium size classes) and prey (juveniles), (2) shifts in size structure of the population (cannibalism takes place mostly on individuals <18·5 cm), which in turn depends on (3) spawning period and (4) variations in other prey abundance (*e.g. M. poutassou*). The density and spatial overlap between age groups often drives cannibalism (Stetter *et al.*, 2007). In the study area, cannibalism occurs between 70 and 200 m depth, which is similar to depths reported by other authors (Kacher & Amara, 2005) and coincides with a predator–prey spatial overlap. The depth distribution of *M. merluccius* in autumn showed a larger and deeper pattern. *Merluccius merluccius* recruits ($L_T < 20$ cm) were found mostly between 100 and 200 m depth. Spawners (>35 cm) displayed a wider depth range; however, they were concentrated on the shelf break and upper slope below 350 m. Similar patterns have been found in other *M. merluccius* populations, such as those in the western Mediterranean Sea (Cartes *et al.*, 2004), central Mediterranean Sea (Carpentieri *et al.*, 2005) and south eastern Atlantic coast of Namibia (Gordoa & Duarte, 1991).

The degree of cannibalism could be partially due to spatial aggregation of resources (trophic aggregations). In this study, cannibalism was higher in nursery areas, where high densities of recruits occur, than outside these areas. A spreading phenomenon outside of these areas, however, was observed in some cases because, although recruits concentrate inside nursery areas (with densities up to 250 individuals per haul), they also extend to adjacent waters. Trophic aggregations were previously noted by Gordoa & Duarte (1991) for two species of hake *Merluccius capensis* Castelnau 1861 and *Merluccius paradoxus* Franca 1960 in Namibian waters. They found a strongly aggregated spatial distribution of medium and small specimens (shallow shoals) and concluded that the formation of aggregations was based on size-dependent shoaling or trophic behaviour. Cartes *et al.* (2004) stated that feeding intensity of *M. merluccius*

was higher in areas of higher concentrations. In this study, populations of *M. merluccius* were found to live in aggregations composed of specimens of different size classes and ages, where juveniles are easily available to large conspecifics. Trophic interactions inside these aggregations may be even more complex because other potential prey, such as *M. poutassou*, coexists with *M. merluccius* populations. *Micromesistius poutassou* is a key prey for *M. merluccius*, but it may also be a competitor of *M. merluccius* recruits because krill (mainly aggregations of the euphausid *Nyctiphanes couchii*) constitutes an essential resource for both fishes. The spatio-temporal coincidence between *M. merluccius* aggregations, *M. poutassou* and krill is strongly related with mesoscale oceanographic processes and should be the subject of future studies.

In the study area, cannibalistic behaviour occurred mainly in pre-adults (predator) between 16 and 30 cm, coinciding with Cartes *et al.* (2009). This is contrary to the results of other authors, who reported that the highest levels of cannibalism were found in larger individuals (Roel & MacPherson, 1988; Carpentieri *et al.*, 2005; Mahe *et al.*, 2007; Ocampo Reinaldo *et al.*, 2011; Link *et al.*, 2012). The recruits and spawners depth pattern found in the study area implies a spatial segregation and could be the main reason for the virtual absence of cannibalism in large specimens.

Because the sampling was conducted in autumn (September and October), the degree of cannibalism was dependent on the size distribution of *M. merluccius* prey and its ability to coexist in time with the predator. Many variables were involved in the occurrence of this spatio-temporal overlap. Among other variables, the spawning period of *M. merluccius* and growth rate could be key factors. Different studies have suggested that the spawning period of this species is very protracted and can even extend over an entire year, although the main spawning peaks have been observed between January and March, with a secondary peak in June and July (Murua & Motos, 2006; Dominguez-Petit *et al.*, 2010; Korta *et al.*, 2010). Recent studies, however, point to more rapid growth than previously thought (Piñeiro *et al.*, 2008). Their analysis of *M. merluccius* recruits (mainly between 8 and 12 cm) sampled in surveys described here would have been born between 76 and 132 days before sampling (based on the formula: $L_T = 3{\cdot}3254A^{0.7336}$, where A is age), *i.e.* during the summer. Although there is still some uncertainty as to this aspect of the biology of this species, the present results suggest that years of high level cannibalism are related to a late spawning period (June to July),when juveniles may reach sizes up to 18 cm in just a few months, according to fast growth models (Piñeiro *et al.*, 2008).

The annual variations in *M. merluccius* cannibalism were also conspicuous. There was huge variability in cannibalism across years. Cannibalism was almost non-existent in 1995 and 1999, while in 2006 and 2008, a substantial increase in cannibalistic behaviour was observed. It is important to note that the increasing cannibalism of 2008 coincided with the depletion of *M. poutassou*, the main prey of *M. merluccius*. Conspecific consumption can increase when other prey are absent (Persson *et al.*, 2000) or unavailable (Post *et al.*, 1998). In recent years, pronounced changes have occurred in the abundance and distribution of some fish species. Two different circumstances should be highlighted: the *M. poutassou* abundance in 2008 represented the minimum historical value of trawl surveys in the southern Bay of Biscay, which coincided with the lowest *M. merluccius* feeding intensity of the entire historical series. This decline was consistent in the whole geographic area. It should be stressed that the size distribution of *M. poutassou* observed in 2008 corresponded to the occurrence of specimens

too large for *M. merluccius* (unpubl. data). Because prey body size represents a key factor in the consumption by a particular predator (Juanes, 2003; Pinnegar *et al.*, 2003; Trenkel *et al.*, 2005), and considering that *M. poutassou* represents a key prey species for *M. merluccius* (Velasco & Olaso, 1998; Preciado *et al.*, 2008), the depletion of *M. poutassou* could be one of the main causes of the changes observed in the diet of *M. merluccius*.

In this study, most of the variations in *M. merluccius* cannibalism were a function of prey density (*M. merluccius* recruits) and were dependent on the density of conspecifics *v.* alternate prey and the relative size difference between juveniles and adults. Although intraspecific spatio-temporal coincidence may be one of the mechanisms employed by fish to regulate the population, there is lack of information on the mechanisms that constrain this adaptive phenomenon.

In conclusion, cannibalism appears to be a characteristic and illustrative behaviour of *M. merluccius* and represents an important source of natural mortality in juveniles. Overall, a high recruitment–high cannibalism pattern was observed, where years of strong recruitment triggered high levels of cannibalism. Generally, the degree of cannibalism depended on the size structure of juveniles, which in turn depended on the spawning period. Some other factors such as food availability for larval growth and oceanographic events (degree of upwelling, currents and mesoscale eddies) may greatly influence recruitment to the bottom. Although outside of the scope of this study, addressing all of these topics should be the next step towards understanding the life history and natural mortality of such an important commercial fish species.

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